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Isolation of Four *RAD23* Genes from *Arabidopsis thaliana* and Detection of Alternative Splicing Variants

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Abstract

DNA damage recognition during nucleotide excision repair (NER) involves the homologous heterodimers Rad4:Rad23 in budding yeast and XPC:hHR23B in human. We report here the characteristics of four *Arabidopsis* homologues of *RAD23* gene, named *AtRAD23-1* to *-4*. *AtRAD23-1*, *-3* and *-4* expressed two alternatively spliced transcripts, long ones (*AtRAD23-1α*, *-3α* and *-4α*) and short ones (*AtRAD23-1β*, *-3β* and *-4β*). The predicted amino acid sequences of these genes possessed four conserved domains of Rad23 family; the ubiquitin-like domain, ubiquitin-associated domain I, XPC-binding domain and ubiquitin-associated domain II. *At*Rad23-3 β and -4 β lacked the C-terminus ubiquitin-like domain and the C-terminus XPC-binding domain, respectively, suggesting that these alternatively spliced variants may modulate functional *At*Rad23 proteins. Phylogenetic analysis showed that plant *RAD23* genes could be divided into two classes and that *Arabidopsis RAD23* genes were recently duplicated. *AtRAD23-1 - 4* transcripts were detected in various tissues, with the highest expression level in flower buds.

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Key words: *Arabidopsis*, Nucleotide excision repair (NER), Rad23.

Abbreviations

ERCC1, excision repair cross-complementing 1; MMS, methyl methane sulfonate; NER, Nucleotide excision repair; RACE, rapid amplification of cDNA ends; RT-PCR, reverse transcriptase-polymerase chain reaction; XPB (C, D, F and G), xeronderma pigmentosum complementation group B (C, D, F and G).

DNA repair systems are very important for all living organisms because DNA damages can block transcription and replication, and eventually result in mutagenesis or cell death. The study of DNA repair mechanisms have been mainly carried out in bacterial, yeast and mammalian cells, but little is known about DNA repair systems in plants.

Plant DNA repair systems have been mainly studied in ultraviolet (UV)-induced DNA damage. Irradiation with short-wavelength UV light induces damage to DNA largely through the formation of cyclobutane pyrimidine dimers (CPDs) and to a lesser extent through the formation of pyrimidine (6-4) pyrimidinone dimers (6-4 photoproducts). The removal of UV-induced DNA damage in plant cells is thought to be a coordinated action of two main

mechanisms, light and dark repairs (Quaite *et al.*, 1994). The former mechanism occurs through the light-dependent repair pathway, which is known as photoreactivation by photolyase (Britt, 1996; Yasui and Eker, 1998). The photoreactivation pathway is mainly recruited in low frequencies of DNA damage. The dark repair pathway is known as nucleotide excision repair (NER), and is mainly recruited in the presence of high frequencies of DNA damage (Costa *et al.*, 2001).

The biological relevance of mammalian NER is well documented, since several human genetic disorders, including xeronderma pigmentosum (XP), Cockayne's syndrome (CS) and trichothiodystrophy (TTD) are associated with defects in NER (Bootsma *et al.*, 1998). NER reaction consists of four major steps and several genes are involved in these processes: *1*) damage recognition (*RAD4* and *RAD23* in budding yeast, *XPC* and *hHR23* in human), *2*) unwinding DNA at the damaged site (*RAD25* and *RAD3* in budding yeast, *XPB* and *XPD* in human), *3*) excision of the damaged DNA by creating incisions on both sides of the lesion (*RAD1, RAD10* and *RAD2* in budding yeast, *XPF, ERCC1* and *XPG* in human), and *4*) gap-filling by DNA polymerase activity (*DNA polymerase* δ and *DNA polymerase* ε in budding yeast and human) and ligation (*DNA ligase I* in budding yeast and human) (Sancar, 1996).

Recently, several NER pathway genes from *Arabidopsis thaliana* have been identified, such as *AtXPB, AtXPD, AtRAD1, AtERCC1, AtRAD2/XPG* and *Arabidopsis DNA ligase I* (Ribeiro *et al.*, 1998; Taylor *et al.*, 1998; Fidantsef *et al.*, 2000; Gallego *et al.*, 2000; Liu *et al.*, 2000, 2001, 2003; Costa *et al.*, 2001; Hefner *et al.*, 2003). Furthermore, mutants of *AtXPB, AtXPD, AtRAD1, AtERCC1* and *AtRAD2/XPG* genes were found to be sensitive to DNA damage such as that induced by UV and/or methyl methane sulfonate (MMS) (Jenkins *et al.*, 1997; Fidantsef *et al.*, 2000; Gallego *et al.*, 2000; Liu *et al.*, 2000, 2001, 2003; Costa *et al.*, 2001; Hefner *et al.*, 2003). Especially the *AtXPD* insertion mutant appears to be lethal, suggesting that *At*XPD is essential in *Arabidopsis* (Liu *et al.*, 2003). However, the roles of other genes involved in NER, such as *RAD23/hHR23* and *RAD4/XPC*, are not well characterized.

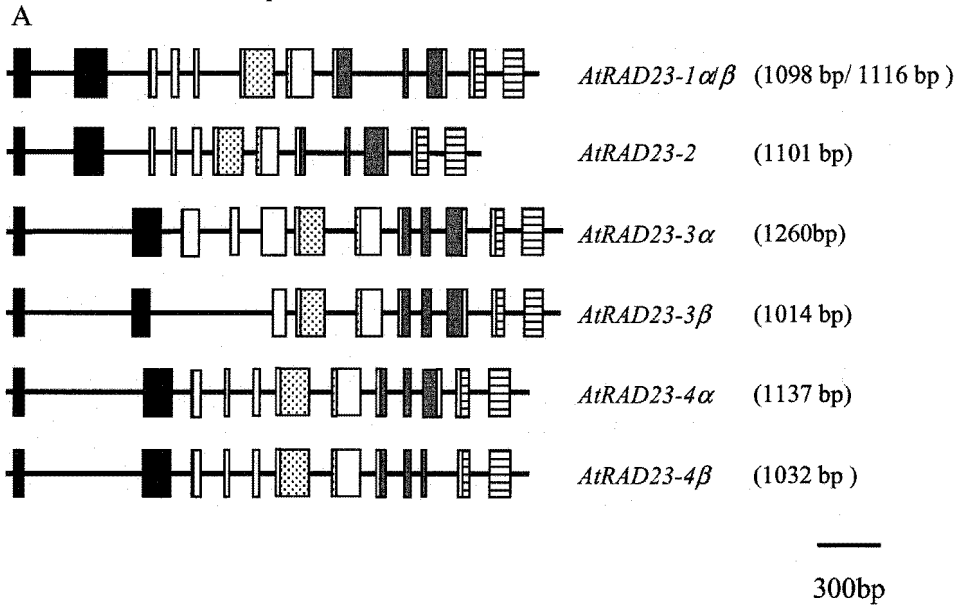
Rad23 from budding yeast and hHR23B from human are involved in DNA damage recognition in NER pathway. Although plant homologs of *RAD23* genes have been reported in rice and carrot (Schultz and Quatrano, 1997; Sturm and Lienhard, 1998), little is known about the function of plant Rad23. *A. thaliana* is a desirable plant for studying NER pathway based on three merits: *1*) the complete sequence of the genome is now available (The Arabidopsis Genome Initiative, 2000), *2*) knock-out lines are currently available, and *3*) the plant NER pathway has been mainly studied in *A. thaliana* (Jenkins *et al.*, 1997; Ribeiro *et al.*, 1998; Taylor *et al.*, 1998; Fidantsef *et al.*, 2000; Gallego *et al.*, 2000; Liu *et al.*, 2000, 2001, 2003; Costa *et al.*, 2001; Wu *et al.*, 2001; Hefner *et al.*, 2003). As a part of studies designed to better understand the NER pathway in plants, we report here the isolation of four members of *RAD23* homologous genes from *A. thaliana*, which were confirmed to be members of the *RAD23* gene based on the *Arabidopsis* genome database. In the present study, we also identified the alternatively spliced transcripts of three of the four *RAD23* homologous genes. We characterized the expression of these genes by northern blot analysis in various plant tissues.

We identified four *RAD23* homologous genes (AY063103, AC010924, AY113034 and AY081835) in the *Arabidopsis* genome database using TBLASTN (http://blast.genome.ad.jp/) with rice and carrot Rad23 protein sequences and named them *AtRAD23-1* to *-4*, respectively. The full-length cDNA sequences of *AtRAD23* genes were cloned by reverse transcriptase-polymerase chain reaction (RT-PCR) and 5′- and 3′-rapid amplification of cDNA ends (RACE) with specific primers designed according to the genomic DNA using cDNA from flower buds. The genome structure of *AtRAD23* genes is shown schematically in **Fig. 1A**. We identified two alternatively spliced transcripts for *AtRAD23-1* (*AtRAD23-1*α and *AtRAD23-1*β), *AtRAd23-3* (*AtRAD23-3*α and *AtRAD23-3*β) and *AtRAD23-4* (*AtRAD23-4*α and *AtRAD23-4*β). In contrast to *AtRAD23-1*, *AtRAD23-3* and *AtRAD23-4*, we could not detect any alternatively spliced transcript for *AtRAD23-2*. The total length and the code for putative protein of the open reading frames (ORFs) of *AtRAD23-1*α and *AtRAD23-1*β were 1116 and 1098 bp, and 371 and 365 amino acids, respectively, with an 18 bp-long deletion in the head of the 4th exon in *AtRAD23-1*β (**Fig. 1B**). The respective values of ORF of *AtRAD23-2* were 1101-bp and 366 amino acids, while those of ORFs of *AtRAD23-3*α and *AtRAD23-3*β were 1260 and 1014 bp and 419 and 337 amino acids, respectively, with a 246-bp long deletion from the end of the 2nd exon of *AtRAD23-3*α to the head of the 4th exon of *AtRAD23-3*α in *AtRAD23-3*β (**Fig. 1A**). The total length and the putative protein of the ORFs of *AtRAD23-4*α and *AtRAD23-4*β were 1137 and 1032 bp and 378 and 343 amino acids, respectively, with a 105-bp deletion from the end of the 10th

exon of *AtRAD23-4α* to the head of the 11th exon of *AtRAD23-4α* in *AtRAD23-4β* (**Fig. 1A**). The *AtRAD23* gene consists of 12 exons and 11 introns except for *AtRAD23-3β* which consists of 10 exons and 9 introns. The predicted *At*Rad23-3 and *At*Rad23-4 proteins from the *Arabidopsis* genome sequencing project [MIPS (Munich information center for protein sequences) *Arabidopsis thaliana* database; http://mips.gsf.de/proj/thal/db/index.html]] were identical with those of *At*Rad23-3α and *At*Rad23-4α. However, the predicted *At*Rad23-1 and *At*Rad23-2 proteins from the MIPS database were incorrect due to misinterpretation of splicing boundaries. *AtRAD23-1α* is an 8-bp deletion due to splicing out at the head of 4th exon of annotated *AtRAD23-1*, a 7-bp insertion due to using a different splicing acceptor site at the end of 4th intron of annotated *AtRAD23-1*, a 7-bp insertion due to using a different splicing acceptor site at the end of 5th intron of annotated *AtRAD23-1*, a 42-bp deletion due to splicing out at the end of 8th exon of annotated *AtRAD23-1* and a 48-bp insertion due to making a new exon (exon 9). In *AtRAD23-2*, the 1st exon exists upstream of the 1st exon of annotated *AtRAD23-2*. *AtRAD23-2* has a 3-bp insertion due to using a different splicing acceptor site at the 1st intron. Also, the annotated *AtRAD23-2* is a deleted 9-12 exons of *AtRAD23-2* due to the use of incorrect stop codon. Recently, we have searched RIKEN Arabidopsis Full-Length Clone Database (Seki *et al.*, 1998; Seki *et al.*, 2002; http://www.brc.riken.go.jp/lab/epd/catalog/cdnaclone.html) and found 3 clones (pda01180, pda01658 and pda05358) which were annotated *Arabidopsis* Rad23. These clones were provided us from RIKEN BIORESOURCE CENTER (http://www.brc.riken.go.jp/lab/epd/Eng/index.html). Sequence analysis of pda01180 revealed that this clone contained completely identical cDNA as *AtRAD23-1α*. Sequence analyses of pda01658 and pda05358 revealed that they also contained completely identical cDNAs as *AtRAD23-4α*.

Motif analysis using the PROSITE database (http://www.expasy.org/prosite/) revealed that amino acids of *At*Rad23-1-4 matched the four distinct conserved domains (ubiquitin-like domain, ubiquitin-associated domain I, XPC-binding domain and ubiquitin-associated domain II) among Rad23 proteins. However, *At*Rad23-3β had 24 amino acids deleted from the C-terminus of ubiquitin-like

A



B

AtRAD23-1α : Exon 3--TTCGGTTCAG**gt**aatttatt-Intron3-agtgtgtc**ag**ACTTCTTCTGTTTCACAGCCTGTTTCCG--Exon 4

AtRAD23-1β : Exon 3--TTCGGTTCAG**gt**aatttatt-Intron3-agtgtgtcagacttcttctgtttcac**ag**CCTGTTTCCG--Exon 4

Fig. 1 A. Schematic genomic structure of *AtRAD23-1α/β, -2, -3α/β* and *-4α/β* genes. Boxes indicate coding exons. Solid boxes: ubiquitin-like domain, dotted boxes: ubiquitin-associated domain I, gray boxes: XPC-binding domain, striped boxes: ubiquitin-associated domain II. Bar indicates nucleotide length (300 bp). B. Genomic DNA sequence of exon-intron junctions of *AtRAD23-1α* and *AtRAD23-1β*. Splice donors (gt) and acceptor sites (ag) are underlined.

Fig. 2 Analysis of the *At*Rad23 derived amino acid sequences. Predicted amino acid sequences were aligned using Clustal W program (Thompson *et al.*, 1994). Comparison of the deduced amino acid sequences of *At*Rad23 proteins with the amino acid sequences of the Rad23 proteins of rice (*Os*Rad23), carrot (*Dc*Rad23-I and-II), tomato (*Le*Rad23), human (*Hs*hHR23B) and budding yeast (*Sc*Rad23p) with four conserved domains (ubiquitin-like domain, ubiquitin-associated domain I, XPC-binding domain and ubiquitin-associated domain II). Asterisks indicate consensus sequences. Accession numbers for 13 deduced amino acids sequences in this analysis are as follows: *At*Rad23-1α (AB109193), *At*Rad23-1β (AB109194), *At*Rad23-2 (AB109195), *At*Rad23-3α (AB109196), *At*Rad23-3β (AB109197), *At*Rad23-4α (AB109198), *At*Rad23-4β (AB109199), *Os*Rad23 (AAB65841), *Dc*Rad23-I (CAA72741), *Dc*Rad23-II (CAA72742), *Le*Rad23 (CAB51544), *Hs*hHR23B (AAN47194) and *Sc*Rad23p (AAB65005).

domain and *At*Rad23-4β lacked 26 amino acids from the C-terminus of XPC-binding domain (**Fig. 2**). *At*Rad23-3β and *At*Rad23-4β may be nonfunctional proteins or have some regulatory role for *At*Rad23-3α and *At*Rad23-4α protein function based on the following: *1*) the ubiquitin-like domain of hHR23 protein, a human homolog of yeast Rad23 protein, interacts specifically with the S5a subunit of the 26S human proteasome (Hiyama *et al.*, 1999), 2) the XPC-binding domain of hHR23 protein interacts with human XPC, and 3) these protein complexes play a role in recognizing DNA damage in NER (Masutani *et al.*, 1997).

We analyzed the relationship between *At*Rad23 proteins and known Rad23 proteins of other species. Similarity between *At*Rad23 proteins was 49 to 81%. High similarities were found between *At*Rad23 proteins and other plant Rad23 proteins (50 to 76%). Phylogeny reconstruction with other known Rad23 proteins revealed that plant Rad23 protein could be divided into two classes (**Fig. 3**). *At*Rad23-1 and *At*Rad23-2 were of the same class that contained *Dc*Rad23-II (carrot). *At*Rad23-3 and *At*Rad23-4 were of the same class that contained *Os*Rad23 (rice), *Dc*Rad23-I (carrot) and *Le*Rad23 (tomato). Other published plants, such as carrot and rice, have one gene in each class, but *A. thaliana* has two copies in each class, suggesting that *Arabidopsis RAD23* genes have duplicated recently in each of these classes.

To determine the tissue-specific expression patterns of *AtRAD23* transcripts, we performed northern blot analysis using *Arabidopsis* poly $(A)^+$ RNA (0.6 μg) from five different tissues: roots, leaves, stems, flower buds and mature flowers (**Fig. 4**). The highest level of expression of *AtRAD23-1* was in flower buds and detected in stems and mature flowers but not in roots and leaves. The highest level of expression of *AtRAD23-2* was in stems and flower buds and detected in mature flowers but not in roots and leaves. *AtRAD23-3* expression was detected in all tissues tested with the highest expression level in stems and flower buds. The expression level of *AtRAD23-4* was similar to that of *AtRAD23*

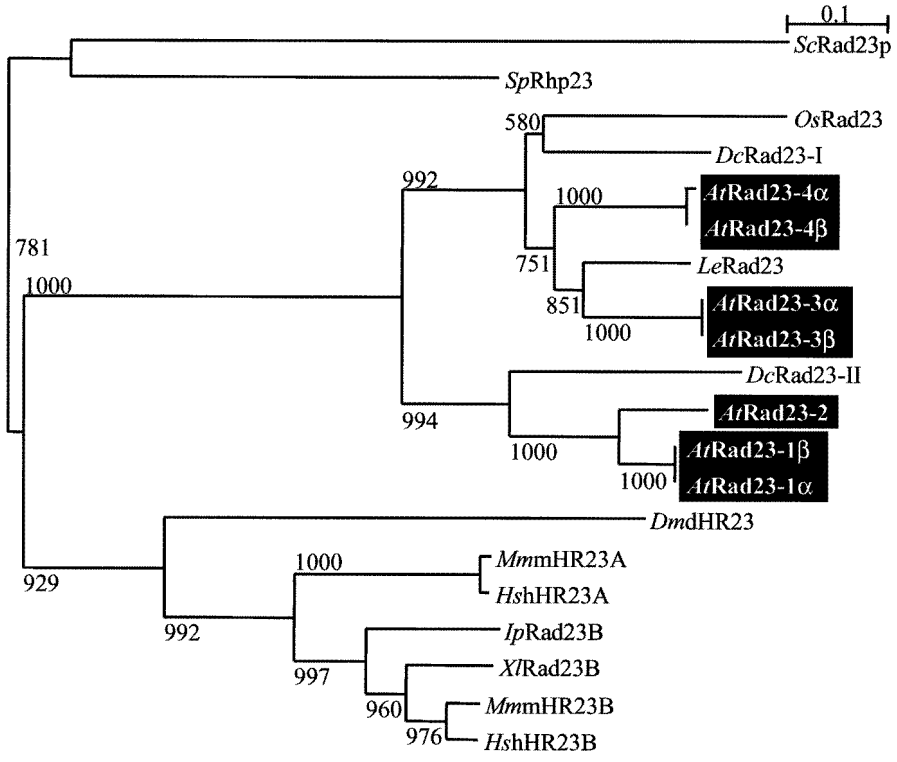


Fig. 3 Phylogeny reconstruction of Rad23 proteins. The Neighbor-Joining tree was generated by Clustal W software. Numbers next to the nodes represent bootstrap values from 1000 replicates. *At*Rad23 proteins are shown in inverted box. Accession numbers of 20 deduced amino acids sequences in this analysis are as follows: *Hsh*HR23A (BAA04767), *Dm*dHR23 (AAD33695), *Mm*mHR23A (CAA63145), *Mm*mHR23B (CAA63146), *Ip*Rad23B (JC7783), *Xl*Rad23B (AAH44115), *Sp*Rhp23 (AAD51975). *At*Rad23-1α, *At*Rad23-1β, *At*Rad23-2, *At*Rad23-3α, *At*Rad23-3β, *At*Rad23-4α, *At*Rad23-4β, *Os*Rad23, *Dc*Rad23-I, *Dc*Rad23-II, *Le*Rad23, *Hsh*HR23B and *Sc*Rad23p were the same as in **Fig 2**. *At-*, *Os-*, *Dc-*, *Le-*, *Sc-*, *Sp-*, *Dm-*, *Mm-*, *Ip-*, *Xl-*, *Hs-* indicate *Arabidopsis*, rice, carrot, tomato, budding yeast, fission yeast, *Drosophila melanogaster*, mouse, *Ictalurus punctatus, Xenopus laevis* and human, respectively.

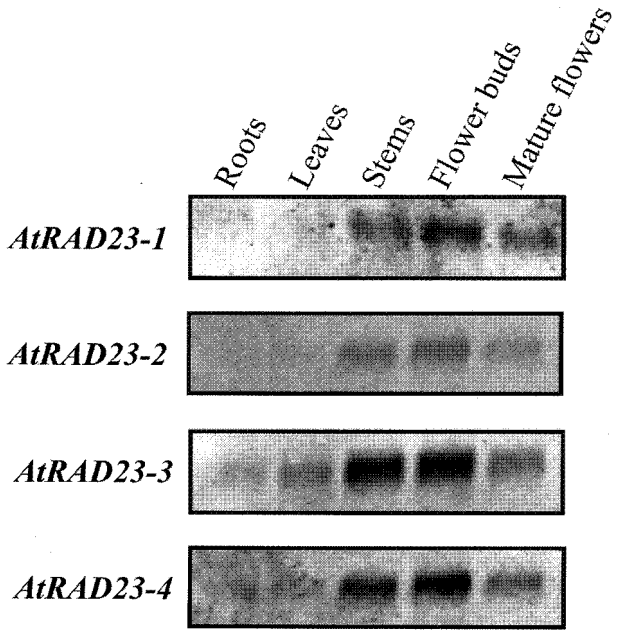


Fig. 4 Northern blot analysis of *AtRAD23* genes in *A. thaliana*. Each lane contains 0.6 μg of Poly $(A)^+$ RNA isolated from the roots, leaves, stems, flower buds, and mature flowers. Specific probes of each *AtRAD23* genes were used for hybridization.

-2. Since the molecular size of each isoform was very close, we could not distinguish isoform α from β. These results resembled the expression patterns of carrot *RAD23* homologous genes that showed the highest expression level in reproductive organs (Sturm and Lienhard, 1998).

To investigate the biological function of *At*Rad23, we screened the T-DNA inserted mutant from Salk Institute Genomic Analysis Laboratory (http://signal.salk.edu/) and identified all *AtRAD23* mutants that have an inserted T-DNA in the exon of each gene (SALK_076036 for *AtRAD23-1*; SALK_066603 for *AtRAD23-2*; SALK_068091 for *AtRAD23-3*; SALK_014137 for *AtRAD23-4*). We are currently analyzing the UV sensitivity of mutants for all *AtRAD23* genes.

Budding yeast Rad23 also forms a strong complex with Rad4 (Guzder *et al.*, 1995), the budding yeast homolog of the XPC protein, required for DNA binding and damaged DNA recognition. We are currently trying to identify *RAD4/XPC* homologous gene for analyzing the function of *AtRAD23* genes and mechanism of NER pathway in plants.

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